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Effect of Russian Wheat Aphid on Yield and Yield Components of Field Grown Susceptible and Resistant Spring Barley

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ABSTRACT

Russian wheat aphid, *Diuraphis noxia* (Mordvilko) (RWA), can be devastating to barley (*Hordeum vulgare* L.) in the western USA. RWA-resistant barley germplasm lines have been developed that control RWA without the use of environmentally detrimental and economically expensive insecticides. This study was conducted to determine if seedling RWA resistance ratings, utilized to develop resistant germplasm lines from greenhouse screenings, accurately predict field performance measured as grain yield and to determine the effect of RWA on yield and yield components of RWA-resistant barley germplasm lines and cultivars differing in seedling RWA resistant rating. Resistant lines and susceptible cultivars were planted at two field locations in Wyoming. Plots were artificially infested with RWA while controls were kept aphid free with pesticide application. Highly resistant lines maintained or increased yield components and grain yield (average grain yield increase 5%) under RWA feeding pressure. Susceptible cultivars had a large reduction in yield components and grain yield (average reduction 56%). The response of moderately resistant and moderately susceptible lines was intermediate and continuous between the resistant and susceptible lines with an average reduction of 20% in grain yield. Seedling resistance ratings accurately predict field performance, providing a more economical, timely, and efficient means of selecting RWA-resistant germplasm lines for release.

Russian wheat aphid can be a devastating pest of barley in the dryland areas of the western USA. Damage symptoms characteristic of RWA infestation include leaf rolling, longitudinal white leaf streaking, purple discoloration, and prostrate growth (Walters et al., 1980; Hewitt et al., 1984). New leaves of infested susceptible plants do not unroll (Burd and Burton, 1992), resulting in trapped and deformed spikes, and reduced grain yield (Robinson, 1994). Aphids feeding inside rolled leaves are protected from contact insecticides. Multiple applications of systemic insecticides, which are costly to the grower and detrimental to the environment, are required for successful chemical control of RWA. Host plant resistance offers the only cost effective means of RWA control, especially in dry arid environments of the western USA where the aphid persists and yields of small grains are generally low.

The RWA was first identified in Texas in 1986. The subsequent rapid spread of the aphid through the intermountain regions of the USA and into Canada by 1988 combined with yield losses in excess of $200 million in wheat and barley (Burton, 1989) resulted in a near panic search for resistance. Greenhouse screenings of all barley cultivars currently grown in the USA revealed all were susceptible to RWA. Because time was critical, and predictable field locations for screening not available, greenhouse screening of the entire USDA-ARS National Small Grains Collection of *Hordeum vulgare* (over 24 000 accessions) was completed from 1990 through 1993 by the USDA-ARS at Stillwater, OK. These screenings identified 109 accessions of barley with some level of resistance to RWA on the basis of Webster's scale of 1 to 9 (Webster et al., 1991). The majority of these accessions were heterogeneous for RWA resistance as well as many agronomic traits. Selection within accessions, by the USDA-ARS in Stillwater, was conducted to produce homogeneous, RWA-resistant, germplasm lines from each of the 109 accessions. These lines fall into two seedling RWA resistance rating classes–resistant (RWA 2–3), where leaves do not streak or roll and moderately resistant to moderately susceptible (RWA 4–6), where leaves do streak and roll but are not killed by the aphid like susceptible plants (RWA 7–9). Two of these germplasm lines have been released to the public, STARS-9301B and Stars-9577B (Mornhinweg et al., 1995, 1999), which were rated 2 and 3, respectively, as seedlings in the greenhouse.

Aphid pressure in typical greenhouse seedling screenings is quite severe. Seedlings are infested as they emerge with a large number of aphids. In the greenhouse, aphids are protected from exposure to parasites and predators common in the field, as well as wind and rain. As a result, aphids build up to great numbers even on flat leaves of resistant seedlings. On the other hand, seedlings in greenhouse flats have ample moisture and nutrients as well as favorable temperatures and are not exposed to natural stresses that may occur in the field during any growing season and which could impact the expression of resistance. Brewer et al. (1998) found RWA ratings based on seedlings in greenhouse predict field grown plant susceptibility to RWA in later growth stages as measured by chlorosis and leaf rolling 67 d (Zadoks 2-tillering) after planting. Bregitzer et al. (2003) found that resistance transferred from STARS 9301B into adapted barley backgrounds protected agronomic performance and malting quality of barley. How accurately RWA resistance ratings of germplasm lines developed from greenhouse screening of seedlings predict resistance measured as grain yield of mature plants in the field has not been reported.

The large number of aphids supported by resistant seedlings in greenhouse screening tests indicates that a major component of resistance in these germplasm lines is tolerance. Although antibiosis and tolerance both play

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a role in the resistance of STARS-9301B, tolerance is the most important (Webster et al., 1991, 1996). A tolerant plant has the ability to grow and reproduce or to repair injury to a marked degree in spite of supporting approximately equal numbers of pests that damage susceptible plants. One way crop plants respond to environmental stress is yield component compensation. Final grain yield in small grains is a product of three yield components–spike number, seeds per spike, and kernel weight. It would be helpful to plant breeders, who will use resistant germplasm in breeding programs, to know what role yield components might play in tolerance to RWA and if that role differs for resistant germplasm lines with varying levels of resistance.

Calhoun et al. (1991) conducted a field study with hill plots of barley genotypes differing in RWA foliar symptom scores (chlorosis and leaf rolling) and determined that expression of foliar symptoms in barley is a good indicator of yield reduction because of RWA feeding. Genotypes with low RWA score (resistant) were higher yielding. They found spike number reduction to be negatively correlated with RWA score and that RWA infestation had no measurable effect on 100-kernel weight. A field study of resistant and susceptible barley genotypes in Mexico (Robinson, 1993) showed decreased grain yield and spike number even in resistant genotypes but less so for resistant than for susceptible genotypes. Kernel weight decreased for both resistant and susceptible genotypes but not with as much difference between resistant and susceptible genotypes as for the other traits. In a separate study, susceptible genotypes were less able to maintain spike number under RWA infestation than resistant types (Robinson, 1994). Bregitzer et al. (2003) showed that trapped spikes of susceptible plants had a marked decrease in fertility and seed size while resistant lines were asymptomatic and had no trapped spikes. Susceptible parents had significant reductions in all agronomic traits including grain yield and kernel weight when infested at an early growth stage. A moderately resistant line preformed better than the susceptible parent but was still greatly affected by RWA infestation. STARS-9301B and four backcross-derived resistant lines showed only small reductions in grain yield and kernel weight compared with susceptible parents.

The literature suggests that the most important contributing factor to yield reduction in small grains attacked by RWA is head trapping, which results from the aphid's inhibition of the unrolling of newly emerging leaves (Burd and Burton, 1992; Robinson, 1994). However, in greenhouse seedling screenings and other tests with high levels of early infestation, seedlings have been shown to die from RWA feeding before new leaves can emerge and before spikes are produced. Tiller death may also be a factor in reduced grain yield in the field.

The objectives of this study were to determine if greenhouse seedling RWA resistance ratings accurately predict field performance in terms of grain yield, to determine the effect of RWA feeding on grain yield and yield components of germplasm lines with differing levels of resistance as well as susceptible cultivars, and to explore the role of yield components in tolerance of RWA-resistant germplasm.

MATERIALS AND METHODS

Fifteen barley germplasm lines, varying in RWA seedling resistance rating from 2 to 6, and four susceptible malting barley cultivars (Table 1), were planted in a randomized complete block design at Laramie and Wheatland, WY, in the spring of 1993 and 1994. The Wheatland location was planted in a commercial cooperator's field and managed according to prevailing practices for malting barley production. The Laramie location was on the University of Wyoming Experiment Station. Two 4-row, 1.5-m-long plots were planted for each entry in each of four blocks. A border row of RWA resistant barley was planted between each plot, and plots were sprinkler irrigated. The center two rows of one plot per entry per block were infested with 10 000 RWA, by the cut leaf method, 4 wk after planting when plants were at the early tillering stage. Control plots were kept aphid-free by applications of methyl parathion (*O,O*-dimethyl *O*-4-nitrophenylphosphorothioate) at the rate of 11.5 L/ha (3 pints/acre) every 2 wk through harvest. RWAs did not establish at the Wheatland site in 1993 because of frequent rains during the 2-wk period following infestation but did establish and were supplemental to a natural infestation at Wheatland in 1994. The plots at the Laramie location were destroyed by a late season hail storm in 1994.

This experiment was cooperative and designed to allow field collection of both agronomic data and entomological data from the same plots. RWAs, companion aphids, and parasites and predators were nondestructively counted on 10 random plants from the center two rows of every plot every 2 wk from infestation through harvest. The results of the entomological studies have been reported (Brewer et al., 1998, 1999). RWA damage was rated on the infested plots by Webster's scale of 1 to 9 at late tillering to early boot stage.

Agronomic measurements, including grain yield (g/0.5 m), number of tillers without spikes, number of tillers with spikes, and number of trapped spikes, were made on one 0.5-m sample harvested from each of the two center rows. Tillers without spikes were those tillers that had begun jointing yet did not live to produce a spike. Data on bird damaged spikes were collected at harvest for each sample at Laramie in 1993 and hail damaged spikes were counted for each sample at Wheatland in 1994. Yield data were not collected from damaged spikes but was instead calculated by multiplying the percentage of normal spikes and percentage of trapped spikes for each sample, by the average grain yield for the normal and trapped spikes in the sample, respectively. Adjusted sample yield was then calculated by summing those yields with the sample yield. Only adjusted sample yield data are reported. Three normal spikes and three trapped spikes were selected from each sample and the number of kernels per spike and kernel weight measured for each spike type. Percentage fertility and 100-kernel weight of normal and trapped spikes were calculated.

PROC MIXED was used to determine which main effects and interactions were significant (SAS, 1999). To avoid confounding effects of location and line in determining the effect of RWA feeding on all traits, multiple comparisons were made on the difference between aphid free and infested means for each line at each location. Significance of multiple comparisons of least-square means was determined by Tukey's adjustment with location, line, and treatment as fixed effects. Pearson's simple correlation coefficients were determined by PROC CORR (SAS, 1999).

Table 1. Origin, row type, greenhouse seedling RWA resistance rating, RWA resistant rating class, and mean number of RWA at each location for each RWA-resistant germplasm line and susceptible barley.

Line	Origin	Row type	Greenhouse seedling RWA resistance rating	RWA resistance class	Mean RWA per 10 tillers Laramie 1993	Mean RWA per 10 tillers Wheatland 1994
STARS 9301B	Afghanistan	6	2	resistant	7.4	0.4
R029	Afghanistan	6	2	resistant	5.6	0.7
R022	Afghanistan	6	3	resistant	5.6	0.4
STARS 9577B	Afghanistan	6	3	resistant	4.6	0.8
MR019	Afghanistan	6	4	moderately resistant	6.8	1.0
MR006	Afghanistan	6	4	moderately resistant	3.3	2.5
MR026	USA	6	5	moderately resistant	15.9	3.3
Gloria/Come	Mexico	6	5	moderately resistant	18.5	5.1
MS004	Greece	6	6	moderately susceptible	11.8	5.4
MS005	Jordan	6	6	moderately susceptible	10.9	2.1
Morex	USA	6	9	susceptible	14.5	2.8
Robust	USA	6	9	susceptible	23.6	7.9
MR013	Egypt	2	4	moderately resistant	10.7	5.3
MR009	Turkey	2	4	moderately resistant	16.4	2.6
MR001	Algeria	2	5	moderately resistant	11.4	2.7
MR028	Algeria	2	5	moderately resistant	12.1	2.1
MS006	France	2	6	moderately susceptible	10.7	4.3
Harrington	USA	2	9	susceptible	22.7	8.2
B1202	USA	2	9	susceptible	37.5	1.6

RESULTS AND DISCUSSION

Haley et al. (2004) reported the discovery of a new biotype of RWA (RWA2) first observed in the summer of 2003 damaging wheat (*Triticum aestivum* L.) cultivars resistant to the original biotype (RWA1) in eastern Colorado. During the time frame of this experiment, it is believed that only RWA1 was present in the testing area. All resistant lines in this study have subsequently been tested in the greenhouse as seedlings for resistance to RWA2 and were found to have the same resistance to this biotype as to RWA1 (data not shown).

Analysis of variance over all locations, lines, and treatments (Table 2) showed the location effect to be significant for all traits except 100-kernel weight, trapped spike kernels per spike, and trapped spike 100-kernel weight. The difference in locations is evidenced by the least squares means of yield and yield components at each location in the absence of RWA (Table 3). The 1994 growing season at Wheatland favored tiller initiation and development compared with conditions at Laramie in 1993. All lines had a higher number of tillers with spikes, fewer tillers without spikes, and higher grain yield at Wheatland. Location × line interaction was significant for all traits except trapped spike kernels per spike, trapped spike 100-kernel weight, and grain yield (Table 2). Location × treatment interaction was significant for tillers with trapped spikes, 100-kernel weight, and grain yield only. Location × line × treatment interactions were significant for tillers with trapped spikes, kernels per spike, and grain yield (Table 2). Because of the significant location effect, locations will be analyzed separately.

The line effect was significant for all traits over all locations, lines, and treatments (Table 2). Least squares means for each line at each location in the absence of RWA (Table 3) demonstrate the considerable differences inherent in six-rowed and two-rowed lines, which could mask the effects of RWA. Six-rowed barleys tiller less, have more kernels per spike, and lower 100-kernel weight than two-rowed barleys. Inherent differences in the susceptible cultivars, which are adapted to the western USA, and the RWA-resistant germplasm lines, developed from accessions from varied areas of the world (Table 1), could also confound conclusions on the effect of RWA on grain yield and yield components. Comparisons between lines will be made on the effect of RWA (aphid free minus infested) for each trait to reduce the confounding effect of lines.

Line × treatment interaction was significant for all traits except tillers with spikes, trapped spike kernels per spike, and trapped spike 100-kernel weight (Table 2). Multiple comparisons of the least-square means of the effect of RWA (aphid free minus infested) for each trait at each location can be found in Tables 4 and 5. At Laramie (Table 4), B1202 and Robust (RWA susceptible) had significant grain yield loss compared with R029 and R022 (RWA resistant), and MR019 and MR001 (RWA moderately resistant), all of which actually showed

Table 2. ***P*** **values of main effects and interactions for grain yield and other traits contributing to grain yield.**

	Tillers without spikes	Tillers with spikes	Tillers with trapped spikes	Kernels per spike	100-kernel weight	Trapped spike kernels per spike	Trapped spike 100-kernel weight	Grain yield
	number		%	number	g	number	g	
Location	0.0005	<0.0001	0.0137	0.0019	0.3369	0.0570	0.6692	<0.0001
Line	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.0123	0.0002	<0.0001
Treatment	<0.0001	0.0005	<0.0001	0.0397	<0.0001	0.2371	0.3074	<0.0001
Location × line	0.0384	0.0008	0.0002	<0.0001	0.0120	0.4694	0.7188	0.0603
Location × treatment	0.1764	0.9426	0.0142	0.3189	0.0453	0.2198	0.6501	0.0036
Line × treatment	0.0003	0.7217	<0.0001	0.0068	<0.0001	0.8858	0.4232	<0.0001
Location × line × treatment	0.9689	0.4861	<0.0001	0.0354	0.5181	0.8956	0.4696	0.0400

Table 3. Least-square means of agronomic traits for each line at Laramie in 1993 and Wheatland in 1994 when aphid free.

	Tillers without spikes		Tillers with spikes		Tillers with trapped spikes		Kernels per spike		100-kernel weight		Grain yield	
Line	1993	1994	1993	1994	1993	1994	1993	1994	1993	1994	1993	1994
	number				%		number		g			
STARS-9301B	13 a†	3 a	64 a	104 bcd	0 a	2 a	34 cd	38 cde	4.02 fg	4.21 efgh	55.77 ab	93.50 a
R029	13 a	3 a	52 a	93 bcd	0 a	4 a	34 cd	39 cd	4.19 efg	4.02 efgh	45.98 ab	74.20 a
R022	26 a	4 a	54 a	92 bcd	1 a	2 a	33 cd	40 cd	4.30 efg	4.45 defgh	50.81 ab	84.19 a
STARS-9577B	17 a	4 a	62 a	103 bcd	0 a	1 a	35 cd	39 cd	4.48 defg	3.78 fgh	59.77 ab	97.69 a
MR019	22 a	2 a	53 a	108 bcd	0 a	2 a	31 def	43 bc	4.00 fg	4.45 defgh	42.13 ab	119.51 a
MR006	23 a	5 a	70 a	93 bcd	1 a	3 a	45 b	48 ab	3.82 gh	3.60 h	65.80 ab	77.46 a
MR013	11 a	1 a	82 a	191 a	3 a	4 a	17 h	18 h	5.79 defg	5.58 abcd	33.42 b	99.21 a
MR009	10 a	1 a	94 a	124 bcd	0 a	4 a	18 gh	16 gh	6.31 a	6.14 a	59.87 b	85.01 a
MR026	3 a	1 a	79 a	114 bcd	1 a	2 a	27 def	34 de	4.94 cde	4.94 bcde	55.10 ab	110.63 a
Gloria/Come	13 a	4 a	57 a	85 c	2 a	9 a	40 bc	40 cd	4.09 fg	3.76 fgh	39.13 b	87.19 a
MR001	8 a	1 a	83 a	138 abc	1 a	3 a	15 gh	16 gh	4.51 bcd	5.40 abcd	37.32 b	81.37 a
MR028	5 a	2 a	57 a	116 bcd	0 a	4 a	17 gh	17 h	5.71 ab	5.75 abc	32.26 b	71.76 a
MS004	16 a	5 a	77 a	106 bcd	3 a	7 a	32 cde	35 de	4.56 defg	4.77 bcdefg	57.65 ab	103.86 a
MS005	8 a	5 a	70 a	87 cd	2 a	5 a	29 def	32 e	4.37 efg	4.48 defgh	38.11 b	82.05 a
MS006	10 a	4 a	69 a	112 bcd	0 a	4 a	16 gh	18 h	5.14 abc	5.83 ab	37.44 b	71.84 a
Morex	12 a	3 a	55 a	83 cd	2 a	4 a	48 ab	51 a	3.94 g	3.50 h	64.74 ab	116.99 a
Robust	8 a	2 a	52 a	73 d	1 a	4 a	53 a	55 a	4.25 efg	3.64 fgh	75.55 ab	113.54 a
Harrington	10 a	5 a	75 a	145 ab	4 a	2 a	24 fg	25 f	4.72 def	4.91 bcdef	48.41 ab	121.62 a
B1202	16 a	6 a	90 a	129 bcd	6 a	7 a	24 efg	24 fg	4.53 defg	4.60 cdefgh	58.76 ab	101.31 a

† Means within columns with different letters are significantly different at the 0.05 level.

grain yield increase with RWA. At Wheatland (Table 5), reduction in grain yield of Harrington (RWA susceptible) was significantly greater than the reduction for 9301B, R029, R022, MR006, MR009, MR013, and MR026. The grain yield of R029 and R022 actually increased. R029 was less affected by RWA feeding than all four susceptible cultivars. The susceptible cultivars had the greatest reductions in grain yield, while three of the highly resistant lines had little or no reduction in grain yield. Grain yield of the intermediate resistant lines fell between the two. Trends in the effect of RWA show highly resistant lines to have either an increase in grain yield or less of a reduction in grain yield than susceptible cultivars, while lines with intermediate resistance fell between the two.

There were no significant differences in lines for tillers with spikes at Wheatland (Table 5) and a significant difference only between B1202 and MR001 at Laramie (Table 4), where B1202 had the greatest reduction in tillers with spikes while MR001 had the greatest increase. Conversely, there were no significant effects of RWA on tillers without spikes at Laramie (Table 4), while Harrington had a significant increase in tillers without spikes compared with all other lines at Wheatland (Table 5). There was a distinct trend among lines for the percentage of tillers with trapped spikes at Wheatland, i.e., the four susceptible cultivars and three moderately susceptible lines had significantly greater percentage of trapped spikes than the four highly resistant lines (Table 5). All four susceptible cultivars had a significantly greater percentage of trapped spikes than the seven moderately resistant lines. With lower levels of resistance, the percentage of tillers with trapped heads increased. At Laramie, all four highly resistant lines had significantly fewer tillers with trapped spikes than three

Table 4. Effect of RWA (aphid free minus infested) on the least-square means of agronomic traits at Laramie in 1993.†

Line	Tillers without spikes	Tillers with spikes	Tillers with trapped spikes	Kernels per spike	100-kernel weight	Trapped spike kernels per spike	Trapped spike 100-kernel weight	Grain yield
	number		%	number	g	number	g	
STARS-9301B	−7 a†	−1 ab	−2 ab	1 ab	0.09 ab	30 abcd	2.78 ab	9.03 ab
R029	0 a	−3 ab	0 a	1 ab	0.04 ab	29 bcd	1.93 b	−9.51 b
R022	10 a	−12 ab	−2 ab	−6 b	−0.33 b	30 abcde	4.15 a	−15.12 b
STARS-9577B	0 a	11 ab	−1 ab	2 ab	0.08 ab	36 abcd	2.01 ab	7.58 ab
MR019	7 a	0 ab	−2 ab	−6 b	−0.29 b	27 abcdef	1.79 ab	−12.42 b
MR006	−18 a	16 ab	−3 abc	13 a	0.79 ab	35 abc	2.56 ab	26.26 ab
MR013	−5 a	5 ab	−10 abcd	0 ab	0.37 ab	7 g	2.61 ab	1.60 ab
MR009	2 a	16 ab	−5 abc	2 ab	0.06 ab	9 g	3.67 a	9.26 ab
MR026	−9 a	21 ab	−25 abcde	2 ab	0.55 ab	22 cdef	1.90 b	22.63 ab
Gloria/Come	−8 a	15 ab	−38 ef	8 ab	0.56 ab	28 bcd	2.42 ab	19.50 ab
MR001	−11 a	−25 b	−10 abc	−2 ab	−0.18 ab	7 g	3.08 ab	−12.36 b
MR028	−2 a	26 ab	−26 bdef	1 ab	0.95 ab	11 fg	2.88 ab	25.58 ab
MS004	−4 a	20 ab	−25 abcde	5 ab	0.82 ab	23 cdef	2.48 ab	28.95 ab
MS005	0 a	25 ab	−36 def	−6 b	0.21 ab	16 defg	1.80 b	7.99 ab
MS006	−6 a	3 ab	−10 abc	0 ab	0.39 ab	13 efg	2.92 ab	2.83 ab
Morex	−9 a	3 ab	−18 abcde	4 ab	0.32 ab	40 ab	1.57 b	14.34 ab
Robust	−4 a	8 ab	−28 cdef	4 ab	0.65 ab	45 a	2.35 ab	40.10 a
Harrington	−22 a	−6 ab	−51 f	1 ab	1.17 a	17 defg	2.49 ab	22.14 ab
B1202	−16 a	29 a	−42 ef	1 ab	1.23 a	18 defg	2.52 ab	38.54 a

† Mean differences within columns with different letters are significantly different at the 0.05 level.

Table 5. Effect of RWA (aphid free minus infested) on the least-square means of agronomic traits at Wheatland in 1994.

Line	Tillers without spikes	Tillers with spikes	Tillers with trapped spikes	Kernels per spike	100-kernel weight	Trapped spike kernels per spike	Trapped spike 100-kernel weight	Grain yield
	number		%	number	g	number	g	
STARS-9301B	0 a†	0 a	0 ab	−2 a	−0.33 ab	26 cd	2.36 abcd	2.43 bc
R029	0 a	−17 a	0 ab	−4 a	0.07 ab	31 c	1.44 cd	−21.58 c
R022	3 a	−2 a	1 a	−1 a	−0.60 b	33 bc	3.18 abcd	−9.20 bc
STARS-9577B	−1 a	13 a	−3 ab	1 a	0.48 ab	26 c	2.55 abcd	20.83 abc
MR019	1 a	4 a	−2 ab	2 a	0.16 ab	32 c	2.39 abcd	21.45 abc
MR006	−4 a	8 a	−17 abcd	0 a	−0.07 ab	34 bc	1.55 cd	11.39 bc
MR013	0 a	16 a	−10 abc	−1 a	−0.07 ab	10 ef	3.73 a	6.35 bc
MR009	2 a	16 a	−8 abc	0 a	0.42 ab	9 f	3.89 a	11.31 bc
MR026	−1 a	16 a	−7 abc	−4 a	0.33 ab	24 cde	2.48 abcd	9.91 bc
Gloria/Come	−3 a	4 a	−18 abcd	2 a	−0.02 ab	25 c	2.35 abcd	17.35 abc
MR001	−3 a	16 a	−20 abcd	0 a	0.46 ab	11 def	3.75 a	20.52 abc
MR028	−2 a	−4 a	−11 abc	0 a	0.54 ab	9 f	3.69 ab	16.15 abc
MS004	−2 a	−1 a	−28 cdef	−2 a	0.37 ab	21 cdef	3.27 abc	23.63 abc
MS005	4 a	10 a	−34 def	−2 a	−0.17 ab	24 cd	1.66 cd	19.88 abc
MS006	0 a	14 a	−22 bcde	0 a	0.18 ab	9 f	3.61 ab	18.62 abc
Morex	−5 a	5 a	−48 fg	4 a	−0.36 ab	48 a	1.33 d	56.72 ab
Robust	−5 a	16 a	−43 efg	2 a	0.33 ab	47 ab	2.20 abcd	64.66 ab
Harrington	−29 b	33 a	−78 h	3 a	1.26 a	21 cdef	2.61 abcd	98.73 a
B1202	−8 a	−4 a	−65 gh	0 a	0.73 ab	21 cdef	1.83 bcd	69.56 ab

† Mean differences within columns with different letters are significantly different at the 0.05 level.

of the susceptible cultivars. The intermediates ranged between the two extremes without a clear trend (Table 4).

There were no significant differences in kernels per spike at Wheatland (Table 5). At Laramie, the reduction in kernels per spike of MR006 was significantly different than the increase in kernels per spike of R022, MR019, and MS005. Trapped spike kernels per spike were greatly reduced for all lines (Tables 4 and 5). The two-rowed lines and cultivars appear to have been less effected by RWA because of their inherent lower kernel number compared with six-row lines and cultivars.

At Wheatland, the reduction in 100-kernel weight of Harrington was significantly different from the increase in 100-kernel weight of R022 (Table 5), while at Laramie, the reduction in 100-kernel weight of Harrington and B1202 was significantly different from the increase in 100-kernel weight of R022 and MR019 (Table 4). Trapped spike 100-kernel weight was reduced for all lines (Tables 4 and 5). The two-rowed lines and cultivars appear to have been more affected by RWA than the 6-row lines and cultivars because of the inherent higher 100-kernel weight of 2-row barleys.

Interpretation of multiple comparisons can be quite difficult especially when dealing with a continuum of values such as the levels of RWA resistance of lines in this experiment. More accurate information can be obtained by correlation coefficients. Correlations between seedling RWA resistance rating class and the effect of RWA (aphid free minus infested) on grain yield and associated traits for each location are shown in Table 6. At Laramie and Wheatland, the effect of RWA on grain yield was significantly and positively correlated with seedling RWA resistance rating class. As seedling RWA resistance rating increased (resistance level decreased), the reduction in grain yield increased. This indicates that seedling RWA resistance ratings accurately predict field resistance in terms of grain yield. At both locations, the effect of RWA on percent of tillers with trapped spikes had the highest correlation with seedling RWA resistance rating class, and the correlation was negative. This supports literature indicating that trapped spikes play a major role in yield loss due to RWA. As resistance level decreased, the percentage of tillers with trapped spikes increased. At Wheatland, the effect of RWA on tillers without spikes was significantly and negatively correlated with seedling RWA resistance rating class, suggesting that under certain environmental conditions tiller death can also contribute to yield loss due to RWA. At Laramie, the effect of RWA on 100-kernel weight was significantly and positively correlated with seedling RWA resistance rating class (Table 6).

Correlations between the effect of RWA (aphid free minus infested) on grain yield and yield components and associated traits for each seedling RWA rating class at each location are given in Table 7. A positive correlation denotes that RWA had the same effect on grain

Table 6. Correlation of Webster's rating (1 to 9) with the difference (aphid free minus infested) of grain yield and traits contributing to grain yield.

	Tillers without spikes	Tillers with spikes	Tillers with trapped spikes	Kernels per spike	100-kernel weight	Grain yield	Trapped spike kernels per spike	Trapped spike 100-kernel weight
	number		%	number	g		number	g
				LARAMIE				
r	−0.2330	0.1733	−0.6273	0.1161	0.4068	0.4490	0.2316	−0.2508
P	0.0428	0.1343	<0.0001	0.3180	0.0003	<0.0001	0.0701	0.0492
				WHEATLAND				
r	−0.4283	0.1535	−0.8426	0.2833	0.2537	0.6170	0.2098	−0.1570
P	0.0001	0.1856	<0.0001	0.0132	0.0270	<0.0001	0.0708	0.1784

Table 7. Correlation of the difference in grain yield (aphid free minus infested) with the difference (aphid free minus infested) in traits that contribute to grain yield for each resistance rating class at each location.

Greenhouse seedling RWA resistance class†	Tillers without spikes	Tillers with spikes	Tillers with trapped spikes	Kernels per spike	100-kernel weight	Trapped spike kernels per spike	Trapped spike 100-kernel weight
	number		%	number	g	number	g
			LARAMIE				
RWA 2–3							
r	−0.1288	0.6048	−0.2666	0.6310	0.6628	0.3691	−0.0478
P	0.6345	0.0131	0.3182	0.0088	0.0051	0.3682	0.9105
RWA 4–6							
r	−0.5015	0.6559	−0.4195	0.6169	0.7070	0.5188	−0.0281
P	0.0005	<0.0001	0.0046	<0.0001	<0.0001	0.0008	0.8672
RWA 9							
r	−0.1415	0.7174	−0.4114	0.4974	0.1958	−0.0313	0.2896
P	0.6012	0.0018	0.1134	0.0499	0.4675	0.9084	0.2766
			WHEATLAND				
RWA 2–3							
r	−0.3729	0.9078	−0.3756	0.8741	0.7166	0.5334	0.5769
P	0.1548	<0.0001	0.1517	<0.0001	0.0018	0.0406	0.0244
RWA 4–6							
r	−0.2088	0.7550	−0.1973	0.5184	0.3838	0.1272	0.2030
P	0.1738	<0.0001	0.1992	0.0003	0.0101	0.4105	0.1863
RWA 9							
r	−0.5284	0.7865	−0.5798	0.4411	0.6268	−0.1837	0.6660
P	0.0354	0.0003	0.0186	0.0872	0.0094	0.4958	0.0048

† Webster's rating 2 to 3 resistant, 4 to 6 moderately resistant to moderately susceptible, 7 to 9 susceptible.

yield and the correlated trait. At Laramie and Wheatland, lines with seedling RWA rating of 2 to 3 showed a high and positive correlation between the effect of RWA on grain yield and yield components (tillers with spikes, kernels/spike, and 100-kernel weight). As tillers with spikes, kernels/spike, and 100-kernel weight increased, so did grain yield. Tolerant, resistant lines maintained or increased grain yield in response to RWA by maintaining or increasing all three yield components. Although kernels per spike and 100-kernel weight of trapped spikes were greatly reduced (Table 4 and 5), there were so few trapped spikes that this did not have an adverse affect on grain yield. Trapped spikes in these plots were rare and could be explained by seed mix in the planting process or perhaps were due to late tillering and head maturation before head extrusion because of temperature or moisture.

Lines with seedling RWA resistance rating of 4 to 6 had significant and positive correlations between the effect of RWA on grain yield and the effect of RWA on tillers with spikes and kernels per spike at Laramie and Wheatland (Table 7). The effect of RWA on 100-kernel weight was positively correlated to the effect of RWA on grain yield at both locations but more significantly at Laramie than Wheatland. These lines varied in their response to RWA and yield components responded to RWA in the same manner. Most moderately resistant and moderately susceptible lines had more trapped spikes than resistant lines (Table 4 and 5). Kernels per spike and 100-kernel weight were greatly decreased in trapped spikes. At Laramie, where tillers with spikes were limited and RWA infestation was greater, trapped spikes and aborted tillers had a more significant effect on grain yield. The effect of RWA on tillers without spikes and the percentage of tillers with trapped spikes were negatively and significantly correlated with the effect of RWA on grain yield. Those tolerant, moderately resistant, or moderately susceptible lines which maintained or increased grain yield in response to RWA had fewer tillers with trapped spikes and fewer tillers without spikes. Those that had reduced grain yield also showed a reduction in yield components as well as an increase in tillers with trapped spikes and tillers without spikes.

The effect of RWA on grain yield of susceptible cultivars was positively correlated with the effect of RWA on tillers with spikes at both locations. Grain yield and tillers with spikes decreased with RWA feeding. At Laramie, where tillering was limited environmentally and aphid populations were high, this was the only significant correlation (Table 7). Such a large percentage of the tillers were trapped that every tiller not trapped was crucial to grain yield. At Wheatland, the effect of RWA on tillers with spikes, 100-kernel weight, and trapped spike 100-kernel weight were significantly and positively correlated to the effect of RWA on grain yield (Table 7). Where conditions were more favorable for tillering, perhaps because of a longer tillering period, an even greater percentage of spikes were trapped and tillers aborted as the aphid populations built up over time, trapping and or killing later tillers. Chlorosis took a negative toll on photosynthate production to the extent that reduction in 100-kernel weight of trapped and normal spikes was significantly and positively correlated with reduction in grain yield.

CONCLUSIONS

Greenhouse seedling RWA resistance ratings accurately predict field performance measured as grain yield. As RWA rating increased (resistance level decreased), the reduction in grain yield increased.

The effect of RWA feeding on grain yield and yield components varies with RWA resistance. Resistant or moderately resistant lines that showed increased grain yield or that maintained grain yield also had an increase in all three yield components. Those moderately resistant and moderately susceptible lines that performed more like susceptible cultivars had a reduction in kernels per spike and 100-kernel weight of spikes, similar to susceptible cultivars, and a greater percentage of tillers with trapped spikes. Yield reduction of susceptible cultivars was accompanied by a reduction in all three yield components but was most highly and negatively correlated with the reduction in tillers with spikes. If a spike is trapped, regardless of seedling RWA resistance rating, the reduction in kernels per spike and 100-kernel weight is large, and the percentage of trapped spikes becomes a major determinant of grain yield loss. At one location, an increase in tillers without spikes was also correlated to grain yield reduction. Yield component response of resistant lines to RWA feeding suggests all three components play a role in tolerance.

Bregitzer et al. (2003) showed a potential for development of high performing RWA-resistant cultivars with the introgression of RWA-resistance from STARS 9301B, suggesting that repeated backcrossing should allow recovery of agronomic performance along with the protection of RWA resistance. The results reported here show that the use of a germplasm line with high seedling RWA resistance (rating of 2 or 3) provides protection against yield loss to RWA under field conditions. All lines rated as moderately resistant do not protect equally against yield loss from RWA, but these lines would have potential value in a breeding program, especially if they have unique genes that may provide resistance to future biotypes of RWA.

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